

# Simultaneous rather than sequential polyandry increases fitness under varying temperature regimes in an aphidophagous ladybird

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**Abstract:** 【Aim】 Although polyandry is common among Coccinellidae, the data attained in various studies are insufficient to explain the general adaptive significance (or fitness consequences) of female remating and polyandry. Temperature was used as a stressor in the study. This study aims to evaluate whether certain benefits of polyandry in terms of increased fitness are also passed on to the progeny. 【Methods】 The present study examined the fitness consequences of three mating treatments in *Coelophora saucia* (Mulsant) (Coleoptera: Coccinellidae): monandry (five matings with same male; one mating/day), sequential polyandry (five matings with five different males with one mating/day with a new male), and simultaneous polyandry (five matings with five males introduced together allowing female to select male to mate; one mating/day). Changes in fecundity and egg fertility, and offspring development and survival of the different mating treatments under different temperatures (25, 27 and 30°C) were observed. 【Results】 The results revealed that females subjected to simultaneous polyandry and thus allowed mate choice or competition amongst males had maximum reproductive performance and offspring best suited to developing and surviving at a wider temperature range. However, sequential polyandrous females had similar reproductive performance as the monandrous female. 【Conclusion】 This indicates that in the absence of mate choice or male competition conditions, benefits of polyandry are not evident. This could be either due to sperm competition amongst subsequent male ejaculates or female cryptic choice. The lack of benefits of polyandry in absence of mate choice as observed in this study has not been previously observed in insects to the best of our knowledge.

**Key words:** Coccinellidae; *Coelophora saucia*; polyandry; mate choice; reproductive performance; offspring fitness

## 1 INTRODUCTION

Most animals (Andersson, 1994; Johnson and Burley, 1997), particularly insects (Arnqvist and Nilsson, 2000), mate more than once in their lifetime. This has multiple costs (loss of time and energy) as well as benefits (increased reproductive output and higher offspring fitness) (Fox 1993a, 1993b; Chapman *et al.*, 1995; Arnqvist and Nilsson, 2000; Omkar and Mishra, 2005a). A cost-benefit analysis predicts that there exists an optimal mating rate (Arnqvist *et al.*, 2004; Omkar *et al.*, 2006a) at which maximal reproductive output is obtained with minimal costs. Multiple matings in nature may be limited to repeated matings with a single male (monandry) but may often involve more than one male (polyandry) (Fuerst *et al.*, 1973; Tregenza and Wedell, 1998; Sakaluk *et al.*, 2002).

Studies have revealed that females in many insect taxa discriminate against previous mates in

support of novel mates by being polyandrous (reviewed by Arnqvist and Nilsson, 2000; Simmons, 2001). A high incidence of polyandry in some species suggests that certain direct and indirect benefits are derived from such behaviour by females (reviewed by Hosken and Stockley, 2003; Simmons, 2005). These may include (1) short term effects, *i. e.*, those that lead to an increase in egg fertility, and (2) long term effects which lead to increased offspring viability, survival, or mating success (Zeh and Zeh, 1997a). Short and/or long term benefits of polyandry have been reported in a number of insects (Tregenza and Wedell, 2002; Omkar and Mishra, 2005b; Srivastava and Omkar, 2005; Mcnamara *et al.*, 2008). Arnqvist and Nilsson (2000) found that polyandry was associated with an increase in reproductive success among species even where males do not provide material benefits to females. But despite all these benefits, monandry still persists in many species likely due to the various costs associated with polyandry, such as increased risk of predation and

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disease transmission, and sometimes even costs associated with toxic properties of male ejaculates (Chapman *et al.*, 1995; Simmons, 2001).

The indirect or genetic benefits derived as a result of polyandry may result in: (1) production of a more genetically diverse set of offspring, usually observed in eusocial insects, and (2) increased offspring fitness in terms of better development, survival, weight, or chances of selection as mates and may be attributed to good male genes or gene compatibility (see the review by Slatyer *et al.*, 2011). The degree of polyandry (number of male mates) also has implications for gene flow (Cheasser and Baker, 1996), speciation (Parker and Partridge, 1998; Gavrilets, 2000) and maintenance of genetic variation (Zeh and Zeh, 1997b). Polyandry can also lead to the evolution of complex behaviour in males and alternative male mating strategies when they are faced with the risk of sperm competition (Arak, 1984; Parker, 1998). A recent meta-analysis on the genetic benefits of polyandry raises the possibility that it is post copulatory sexual selection by the female which is more likely to result in good or compatible gene benefits than female choice of mates (Slatyer *et al.*, 2011). In a number of polyandrous insects (Fox and Hickman, 1994; Ivy and Sakaluk, 2007) including ladybirds (Omkar and Mishra, 2005b; Srivastava and Omkar, 2005), while polyandry gives better reproductive output than monandry, mate choice further enhances these benefits.

Change in temperature is known to affect reproductive and sexually selected traits (Chihirane and Lauge, 1994; West and Packer, 2002) and it is likely that mating costs and benefits are also sensitive to it. In male eastern mosquitofish, *Gambusia holbrooki*, mating performance was influenced at extreme temperatures (Wilson, 2005). Also, mating success in butterflies has been found to change with both developmental and acclimation temperatures (Geister and Fischer, 2007). A recent study by Grazer and Martin (2012) on *Tribolium castaneum* revealed increased reproductive success as a benefit of polyandrous condition at elevated temperatures. Ladybirds are known to show significant differences in growth, development, survival and reproduction even at narrow range of temperatures (25, 27 and 30°C) under laboratory conditions (Pervez and Omkar, 2004; Omkar and Pervez, 2004), with 30°C being lethal for eggs in some ladybirds (Lombaert *et al.*, 2008). Earlier, two studies, on a coccinellid and a chrysomelid have evaluated the effect of range of temperatures on development and survival of offspring of monandrous and polyandrous mate choice pairs (Omkar

and Mishra, 2005b). They found that offspring of polyandrous pairs were able to survive better at a range of temperatures than those of the monandrous ones.

In view of the possible modulating effects of temperature on mating and reproductive success, the present study assessed the effect of (i) polyandry on a new ladybird, *Coelophora saucia* (Mulsant) and (ii) temperature as a stressor on its offspring to assess their fitness levels as indicators of indirect benefits of polyandry. Earlier studies on polyandry have been conducted in ladybirds, *Propylea dissecta* (Mulsant), *Adalia bipunctata* (L.) and *Coccinella septempunctata* (L.). The ladybirds, in which polyandry has been studied, are in a range of sizes and mating behaviour, both of which may influence mating outcomes. While *P. dissecta* is a small species which reportedly does not transfer a spermatophore (Omkar and Pervez, 2005), *A. bipunctata* is a small ladybird with spermatophore ejection and consumption (Majerus, 1999), *C. septempunctata* is a medium sized beetle with spermatophore ejection and consumption (Obata and Johki, 1991; Omkar and Srivastava, 2002). *Coelophora saucia* is a large beetle with no observed spermatophore ejection and consumption, different from previous ladybirds studied, thus, warranting its selection as a model. This ladybird mates once per day (Omkar *et al.*, 2010) and deviations from this pattern occur only when males have not been allowed to mate for long and are then confined with one female resulting in more vigorous and frequent mating. In India, this polymorphic species is commonly found in colonies of *Aphis craccivora* Koch (Saharia, 1980; Omkar *et al.*, 2005) and sugarcane woolly aphid, *Ceratovacuna lanigera* Zehntner (Joshi and Viraktamath, 2004; Singh and Tripathi, 2008). Only the effect of increased mating duration on fecundity and egg viability has been previously studied in *C. saucia* (Omkar *et al.*, 2006b). This study was undertaken to assess the potential benefits of polyandry and to test the hypotheses that: (i) both sequential and simultaneous polyandry will result in increased fecundity, egg fertility, and offspring fitness in comparison to monandry, (ii) mate choice would enhance the above benefits of polyandry, and (iii) offspring sired by polyandrous parents would be able to cope better with temperature variations.

## 2 MATERIALS AND METHODS

### 2.1 Stock maintenance

Adults of *C. saucia* were collected from bean (*Dolichos lablab* Linnaeus) fields infested with

aphid, *A. craccivora* located in the suburbs of Lucknow, India. They were paired in Petri dishes (9.0 cm × 2.0 cm; one mating pair per Petri dish) and reared on an *ad libitum* supply of above prey under laboratory conditions (25 ± 2°C, 65% ± 5% R. H., 14L: 10D in Environmental Test Chamber, Remi Instruments). Eggs laid were separated daily and the hatched instars reared until pupation in glass beakers (11.0 cm × 5.0 cm; 10 neonates per beaker) on *ad libitum* supply of *A. craccivora* infested on *D. lablab*. Newly emerged adults were placed individually in Petri dishes (9.0 cm × 2.0 cm) till they were required for the experiments.

## 2.2 Experimental design

**2.2.1 Influence on reproduction:** To investigate the effects of polyandry on reproductive performance of *C. saucia*, experiments were designed following Sakaluk *et al.* (2002) and Omkar and Mishra (2005b). This experimental design has been considered appropriate and rigorous by Slatyer *et al.* (2011) in their meta-analysis for estimating genetic benefits of polyandry. The experimental treatments were: (A) 5-day-old virgin female paired with a 5-day-old unmated male that was removed daily after a single mating, thus allowing only five matings for five days with the same male (monandry), (B) 5-day-old virgin female was provided daily sequentially with a new male for a single mating (each male had age and mating status similar to that of the female on the day of mating), thus allowing five matings with five different males in five days (sequential polyandry), and (C) 5-day-old female provided simultaneously with five 5-day-old unmated males on day 1 of study, thus allowing freedom to choose mate as well as male competition (simultaneous polyandry, mate choice/competition). Unmated males in treatment (C) were removed after the female had established genital contact, while the mating male was removed post mating. All five males were reintroduced into the arena the next day. Females in each treatment mated once daily. All these treatments were set up in Petri dishes (9.0 cm × 2.0 cm) and were provided daily with fresh *ad libitum* *A. craccivora* infested on *D. lablab* twigs. All females used in the experiments weighed 35.00 ± 2.50 mg while males weighed 25.00 ± 2.50 mg, and this was done to ensure lack of variation in male and female quality due to size. After the mating treatments, males were removed and females were observed for the next 20 days for daily oviposition and percent egg viability. The experiment was conducted in ten replicates per treatment with a pair in a single Petri dish forming a replicate.

**2.2.2 Influence on offspring fitness:** For evaluating the effect of polyandry on offspring fitness of *C. saucia*, the development and survival of progeny of the three treatments in (I) was studied at three different temperatures, *i. e.* 25, 27 and 30°C. Fifty eggs laid between 10:00 – 12:00, 24 hours after completion of all three treatments in 2.2.1 were selected randomly and placed at one of these three temperatures. The hatched neonates were placed in beakers (9.5 cm × 6.5 cm) covered with muslin fastened with a rubber band along with *ad libitum* *A. craccivora* on host plant. Five neonates were placed per beaker to avoid overcrowding, with one beaker constituting a replicate. The total developmental time (from egg to adult emergence) and the numbers of adults emerging were recorded. Since there were five instars per beaker, the mean values per beaker were considered as the observation of a replicate. Observations were taken at 12-hour intervals. No cannibalism was observed in any replicate probably owing to *ad libitum* aphid supply and presence of host plant twigs and leaves which allowed enough area to roam and hide, thereby reducing interactions.

## 2.3 Statistical analysis

All data were checked for normality and heterogeneity of variance following Kolmogorov-Smirnov's and Bartlett's test and found to be normally distributed with homogeneity of variances. Percentage data were subjected to arcsine square root transformation before being subjected to analysis. Data on fecundity and percent egg viability were subjected to one-way ANOVA and *post hoc* comparison of means using Tukey's test of significance on statistical software MINITAB (2000).

To examine the effects of polyandry and offspring rearing environment, the data were subjected to two-way ANOVA with mating treatments and temperature regimes as independent factors followed by *post hoc* comparison of means using Tukey's test of significance. All analyses were done using statistical software MINITAB (2000).

# 3 RESULTS

## 3.1 Influence of polyandry on reproduction of *C. saucia*

Simultaneous polyandrous females were found to lay maximum number of eggs and the overall difference amongst treatments was statistically significant ( $F_{2,26} = 12.05$ ;  $P = 0.001$ ) (Fig. 1). However, comparison of means revealed that there were no significant differences between the females subjected to monandry and sequential polyandry.

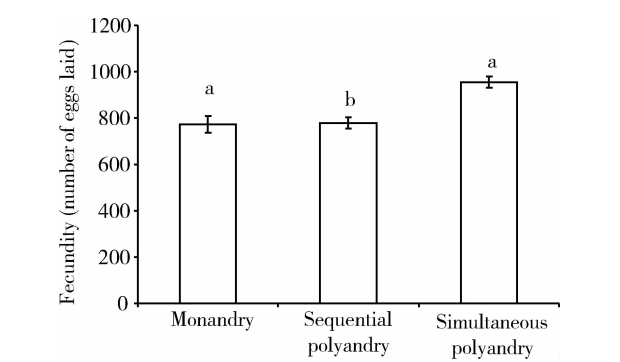


Fig. 1 Effect of polyandry on fecundity of *Coelophora saucia*. Values are means  $\pm$  SE. Different letters denote significant differences in a parameter between treatments using ANOVA followed by Tukey's *post hoc* analysis at  $P < 0.05$ . The same for the following figures.

The percent egg viability was also highest in the eggs oviposited by simultaneous polyandrous females and there were overall statistically significant differences in the treatments ( $F_{2,26} = 9.29$ ;  $P = 0.004$ ) (Fig. 2). Minimum percent egg viability was recorded in monandrous females. The individual comparison of means revealed that egg viabilities in monandrous and sequential polyandrous, and sequential polyandrous and simultaneous polyandrous did not differ significantly from each other. However, there was statistically significant difference between monandrous and simultaneous polyandrous conditions (Fig. 2).

3.2 Influence of polyandry on offspring fitness of *C. saucia*

Two-way ANOVA revealed that total developmental time was unaffected by the mating treatments ( $F_{2,81} = 2.31$ ;  $P = 0.06$ ) and percent adult

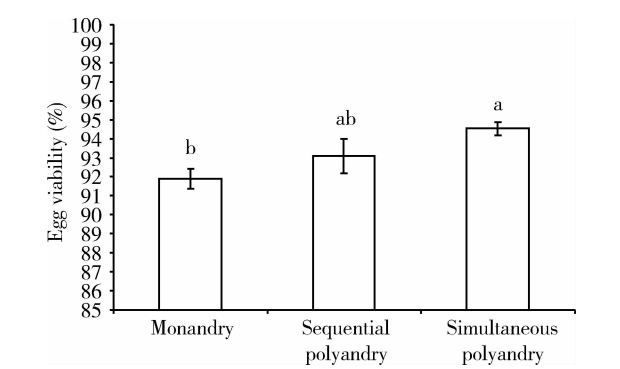


Fig. 2 Effect of polyandry on percent egg viability of *Coelophora saucia*

emergence was significantly influenced ( $F_{2,81} = 4.03$ ;  $P = 0.02$ ). Both total developmental period ( $F_{2,81} = 151.23$ ;  $P = 0.001$ ) and percent adult emergence ( $F_{2,81} = 8.17$ ;  $P = 0.001$ ) were significantly influenced by the different temperature regimes (Table 1). The interaction was insignificant between the mating treatments and temperature for both total developmental period ( $F_{4,81} = 1.02$ ,  $P = 0.326$ ) and percent adult emergence ( $F_{4,81} = 0.71$ ;  $P = 0.476$ ). *Post hoc* comparison of means revealed that at each temperature, there was no significant difference in developmental time of immature stages of each mating treatment. Development of immature stages of each mating treatment was fastest at 30°C (Fig. 3). Percent adult emergence was significantly higher in offspring of simultaneous polyandry treatment at each temperature (Fig. 4). Maximum adult emergence was observed at 27°C in each mating treatment.

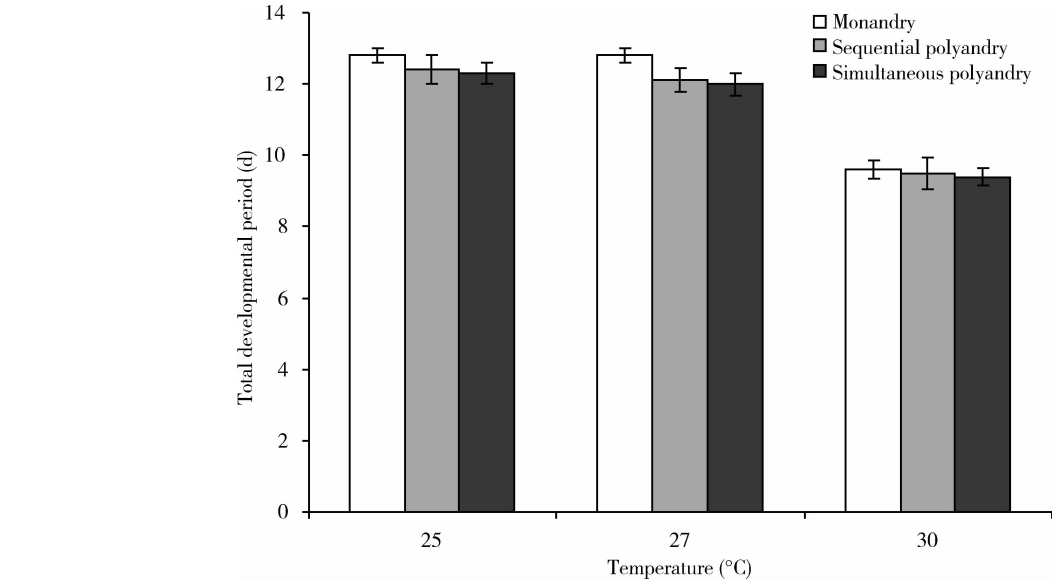


Fig. 3 Effect of polyandry on the total developmental period of *Coelophora saucia*

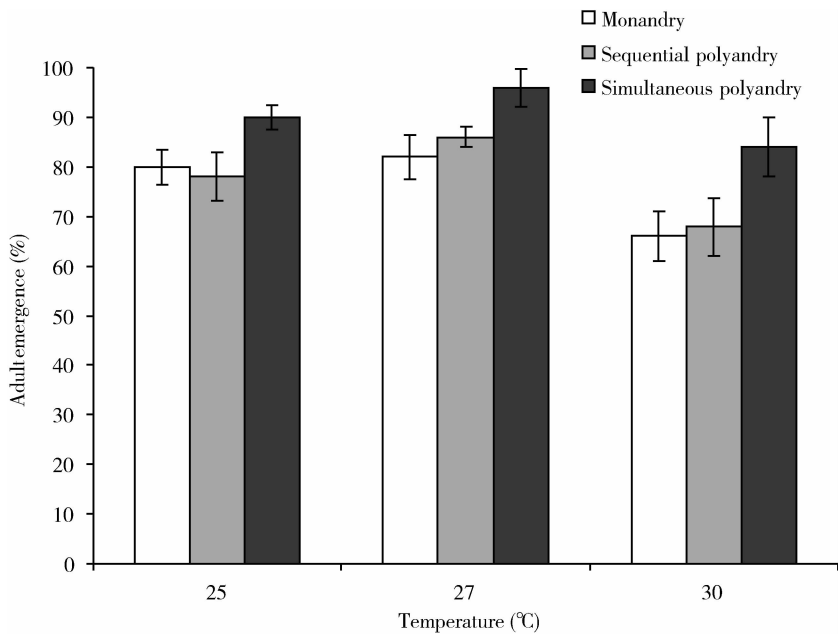


Fig. 4 Effect of polyandry on percent adult emergence of *Coelophora saucia*

**Table 1** Effect of mating treatments and temperature regimes on offspring fitness in *Coelophora saucia*

Variable	Source	df	MS	F	P value
Developmental time	Mating treatment	3	1.24	2.97	0.041
	Temperature regime	2	69.78	167.47	0.001
	Treatment × Temperature	6	0.48	1.15	0.349
Adult emergence	Mating treatment	3	446	3.52	0.022
	Temperature regime	2	1 152	9.09	0.001
	Treatment × Temperature	6	116	0.92	0.491

## 4 DISCUSSIONS

The study reveals that polyandry influences both the reproduction and offspring fitness of *C. saucia* only when simultaneous choice/competition conditions are provided. In the absence of such conditions no significant difference was recorded between monandrous and sequential polyandrous treatments. These are rather interesting but unexpected results as most studies on polyandry reveal significant differences between monandrous and polyandrous treatments even in the absence of such conditions.

The absence of statistically significant difference amongst the reproductive performance of sequential polyandrous and monandrous females goes against our hypothesis that serial matings with new males would increase fecundity as a probable result of increased nutrient supply and/or presence of oviposition stimulants in the ejaculate (Wedell and Ritchie, 2004; Torres-Vila and Jennions, 2005). All the ladybirds in which polyandry has been

previously studied, have shown increase in egg output and viability when mated with new males (de Jong *et al.*, 1998; Omkar and Mishra, 2005b; Srivastava and Omkar, 2005). Mating with unmated males is expected to increase the viability due to increased sperm supply by them (Preston *et al.*, 2001; Montrose *et al.*, 2004; Harris and Moore, 2005; Edvardsson *et al.*, 2008). Also, studies on male mating status in other insects have shown that females are able to change their choices and prefer unmated males over mated ones (Harris and Moore, 2005; Ivy *et al.*, 2005).

The better reproductive performance of polyandrous treatment allowing mate choice/male competition could be attributed to (a) repeated selection of unmated males leading to increased sperm supply, (b) the freedom to choose and mate repeatedly with the better male, and/or (c) male competition permitting the better male to mate and remate. The quality and quantity of male ejaculate size are known to be determined by genetic composition and intra- as well as inter-specific variations (Boake, 1994; Aragaki and Meffert, 1998; Radwan, 1998; Sakaluk and Smith, 1998; Savalli *et al.*, 2000; Schaus and Sakaluk, 2002). It is well established that female fitness is most likely to be negatively affected if her eggs are fertilized by males of poor health and bad vigour or bad genes (Keller and Reeve, 1995; Yasui, 1997, 1998; Andersson and Simmons, 2006; Evans and Simmons, 2008). Such a situation is usually avoided through selection of males which may be

done by various selection mechanisms at the premating stage or through the use of cryptic female choice post mating (Andersson, 1994; Eberhard, 1996; Andersson and Simmons, 2006). In captive ladybird females, the males are known to force mating despite female resistance (Pervez *et al.*, 2004; Srivastava and Omkar, 2005; Omkar and Pervez, 2005), leading to a situation where female can employ cryptic female choice for male selection. Thus, in ladybirds, it is likely that females might allow preferential fertilization of her eggs with sperm of better male through the process of cryptic female choice (Birkhead and Møller, 1993; Eberhard, 1996; Birkhead, 1998; Fedina and Lewis, 2007; Ward *et al.*, 2008). It is also possible that ladybirds might not choose mates but rather there may be competition between males for mates. Even in this scenario, the better and more vigorous male is likely to succeed and thus the same benefits would be evident as in the case of mate choice.

Offspring of simultaneous polyandrous females survived maximally at the three temperatures revealing them to be better at dealing with environmental stresses. This supports our presumption that when allowed mate choice/male competition the females are mating with the fitter males. In ladybirds, *P. dissecta* and *C. septempunctata*, parental mating histories were found to influence the fitness of offspring (Omkar and Mishra, 2005b; Srivastava and Omkar, 2005). Influence of environmental factors has previously been studied in crickets with nutrition deprivation acting as a stressor (Sakaluk *et al.*, 2002). Male mating history did not affect the offspring ability in terms of developmental time and survival in dealing with nutritional stress (Sakaluk *et al.*, 2002), though, adult male offspring of polyandrous females were significantly larger and heavier in weight (Sakaluk *et al.*, 2002). This is important in cases where larger males are preferred over smaller ones as mates (Sakaluk, 1984, 1985; Souroukis and Cade, 1993; Bateman *et al.*, 2001). A limitation of the current study was the inability to recognize the parentage of the offspring. It could be possible that all the eggs might have been sired by one male or multiple ones in both the polyandrous setup, affecting their performance.

The study thus reveals that simultaneous polyandry in ladybird, *C. saucia* due to mate choice/male competition conditions leads to increased (i) reproductive performance, and (ii) better adaptability of the offspring in countering environmental stresses. However, in the absence of

choice/competition conditions, sequential polyandry shows no benefits of polyandry and has reproductive and offspring performance similar to that of monandrous females.

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## References

- Andersson M, 1994. Sexual Selection. Princeton University Press, Princeton New Jersey.
- Andersson M, Simmons LW, 2006. Sexual selection and mate choice. *Trends Ecol. Evol.*, 21: 296–302.
- Aragaki DL, Meffert LM, 1998. A test of how well the repeatability of courtship predicts its heritability. *Anim. Behav.*, 55: 1141–1150.
- Arak A, 1984. Sneaky breeders. In: Barnard CJ ed. Producers and Scroungers. Croom-Helm, London. 154–194.
- Arnqvist G, Nilsson T, 2000. The evolution of polyandry: multiple mating and female fitness in insects. *Anim. Behav.*, 60: 145–164.
- Arnqvist G, Nilsson T, Katvala M, 2004. Mating rate in female weevils. *Behav. Ecol.*, 16: 123–127.
- Bateman PW, Gilson LN, Ferguson JWH, 2001. Male size and sequential mate preference in the cricket, *Gryllus bimaculatus*. *Anim. Behav.*, 61: 631–637.
- Birkhead TR, 1998. Cryptic female choice: criteria for establishing female sperm choice. *Evolution*, 52: 1212–1218.
- Birkhead TR, Møller AP, 1993. Female control of paternity. *Trends Ecol. Evol.*, 8: 100–104.
- Boake CRB, 1994. Repeatability: its role in evolutionary studies of mating behaviour. *Anim. Behav.*, 3: 173–182.
- Chapman T, Liddle LF, Kalb JM, Wolfner MF, Partridge L, 1995. Cost of mating in *Drosophila melanogaster* female is mediated by male accessory gland products. *Nature*, 373: 241–244.
- Cheasser RK, Baker RJ, 1996. Effective sizes and dynamics of uniparentally and diparentally inherited genes. *Genetics*, 144: 1225–1235.
- Chihirane J, Lauge G, 1994. Effects of high-temperature shocks on male germinal cells of *Trichogramma brassicae* (Hymenoptera: Trichogrammatidae). *Entomophaga*, 39: 11–20.
- de Jong PW, Brakefield PM, Geerinck BP, 1998. The effect of female mating history on sperm precedence in the two-spot ladybird, *Adalia bipunctata* (Coleoptera: Coccinellidae). *Behav. Ecol.*, 9 (6): 559–565.
- Eberhard WG, 1996. Female Control: Sexual Selection by Cryptic Female Choice. Princeton University Press, Princeton, New Jersey.
- Edvardsson M, John H, Moore PJ, Moore AJ, 2008. Female agreement over male attractiveness is not affected by cost of mating with experienced males. *Behav. Ecol.*, 19: 854–859.

- Evans JP, Simmons LW, 2008. The genetic basis of traits regulating sperm competition and polyandry: can selection favour the evolution of good-and sexy-sperm? *Genetica*, 134: 5 – 19.
- Fedina TY, Lewis SM, 2007. Female mate choice across mating stages and between sequential mates in flour beetles. *J. Evol. Biol.*, 20: 2138 – 2143.
- Fox CW, 1993a. Multiple mating lifetime fecundity and female mortality of the bruchid beetle, *Callosobruchus maculatus* (Coleoptera: Bruchidae). *Funct. Ecol.*, 7: 203 – 208.
- Fox CW, 1993b. The influence of maternal age and mating frequency on egg size and offspring performance in *Callosobruchus maculatus* (Coleoptera: Bruchidae). *Oecologia*, 96: 139 – 146.
- Fox CW, Hickman DL, 1994. The influence of oviposition substrate on female receptivity to multiple mating in *Callosobruchus maculatus* (Coleoptera: Bruchidae). *Ann. Entomol. Soc. Am.*, 87: 395 – 398.
- Fuerst PA, Pendleury WW, Kidwell JF, 1973. Propensity for multiple mating in *Drosophila melanogaster* females. *Evolution*, 27: 265 – 268.
- Gavrilets S, 2000. Rapid evolution of reproductive barriers driven by sexual conflict. *Nature*, 403: 886 – 889.
- Geister TL, Fischer K, 2007. Testing the beneficial acclimation hypothesis: temperature effects on mating success in a butterfly. *Behav. Ecol.*, 18(4): 658 – 664.
- Grazer VM, Martin OY, 2012. Elevated temperature changes female costs and benefits of reproduction. *Evol. Ecol.*, 26(3): 625 – 637.
- Harris WE, Moore PJ, 2005. Female mate preference and sexual conflict: females prefer males that have had fewer consorts. *Am. Nat.*, 165: 564 – 571.
- Hosken DJ, Stockley P, 2003. Benefits of polyandry: a life history perspective. *Evol. Biol.*, 33: 173 – 194.
- Ivy TM, Sakaluk SK, 2007. Sequential mate choice in decorated crickets: females use a fixed internal threshold in pre- and postcopulatory choice. *Anim. Behav.*, 74: 1065 – 1072.
- Ivy TM, Weddle CB, Sakaluk SK, 2005. Females use self-referent cues to avoid mating with previous mates. *Proc. R. Soc. Lond. B*, 72: 2475 – 2478.
- Johnson K, Burley NT, 1997. Mating tactics and mating systems of birds. In: Parker PG, Burley NT eds. *Avian Reproductive Tactics: Female and Male Perspectives Ornithological Monographs*. American Ornithologist's Union, Washington DC. 21 – 60.
- Joshi S, Viraktamath CA, 2004. The sugarcane woolly aphid *Ceratovacuna lanigera* Zehntner (Hemiptera: Aphididae): its biology, pest status and control. *Current Science*, 87: 307 – 316.
- Keller L, Reeve HK, 1995. Why do females mate with multiple males? The sexually selected sperm hypothesis. *Adv. Stud. Behav.*, 24: 291 – 315.
- Majerus MEN, 1999. Spotting the darker side of ladybirds. *Biologists*, 46: 109 – 113.
- McNamara KB, Brown RL, Mark AE, Jones TM, 2008. Paternity costs from polyandry compensated by increased fecundity in the hide beetle. *Behav. Ecol.*, 19: 433 – 440.
- Montrose VT, Harris WE, Moore PJ, 2004. Sexual conflict and cooperation under naturally occurring male sequential monogamy. *J. Evol. Biol.*, 17: 443 – 452.
- Moya-Larano J, Fox CW, 2006. Total ejaculate size second male body size and moderate polyandry increase female fecundity in a seed beetle. *Behav. Ecol.*, 17: 940 – 946.
- Obata S, Johki Y, 1991. Comparative study on copulatory behaviour in four species of aphidophagous ladybirds. In: *Proceedings of 4th Meeting of the IOBC WG Ecology of Aphidophaga*, Hungary. 207 – 212.
- Omkar, Mishra G, 2005a. Mating in aphidophagous ladybirds: costs and benefits. *J. Appl. Entomol.*, 129: 432 – 436.
- Omkar, Mishra G, 2005b. Evolutionary significance of promiscuity in an aphidophagous ladybird, *Propylea dissecta*. *Bull. Entomol. Res.*, 95: 527 – 533.
- Omkar, Mishra G, Singh SK, 2006a. Optimal number of matings in two aphidophagous ladybirds. *Ecol. Entomol.*, 31: 1 – 4.
- Omkar, Pervez A, 2005. Mating behaviour of an aphidophagous ladybird beetle, *Propylea dissecta* (Mulsant). *Insect Sci.*, 12: 37 – 44.
- Omkar, Pervez A, Singh SK, 2005. Development and immature survival of two aphidophagous ladybirds, *Coelophora biplagiata* and *Micraspis discolor*. *Insect Sci.*, 12: 375 – 379.
- Omkar, Singh K, Pervez A, 2006b. Influence of mating duration on fecundity and fertility in two aphidophagous ladybirds. *J. Appl. Entomol.*, 130: 103 – 107.
- Omkar, Singh SK, Mishra G, 2010. Multiple matings affect the reproductive performance of an aphidophagous ladybird beetle, *Coelophora saucia*. *Eur. J. Entomol.*, 107: 177 – 182.
- Omkar, Srivastava S, 2002. The reproductive behaviour of an aphidophagous ladybeetle, *Coccinella septempunctata* Linnaeus. *Eur. J. Entomol.*, 99: 465 – 470.
- Parker GA, 1998. Sperm competition and the evolution of ejaculates: towards a theory base. In: Birkhead TR, Møller AP eds. *Sperm Competition and Sexual Selection*. Academic Press, London. 3 – 54.
- Parker GA, Partridge L, 1998. Sexual conflict and speciation. *Phil. Trans. R. Soc. B*, 353: 261 – 274.
- Pervez A, Omkar, Richmond AS, 2004. The influence of age on reproductive performance of a predatory ladybird beetle, *Propylea dissecta*. *J. Insect Sci.*, 4: 1 – 8.
- Preston BT, Stevenson IR, Pemberton JM, Wilson K, 2001. Dominant males lose out by sperm depletion. *Nature*, 409: 681 – 682.
- Radwan J, 1998. Heritability of sperm competition success in the bulb mite, *Rhizoglyphus robini*. *J. Evol. Biol.*, 11: 321 – 327.
- Saharia D, 1980. Natural regulation of population of *Aphis craccivora* Koch on cowpea. *Journal of Research by Assam Agricultural University*, 1: 171 – 176.
- Sakaluk SK, 1984. Male crickets feed females to ensure complete sperm transfer. *Science*, 223: 609 – 610.
- Sakaluk SK, 1985. Spermatophore size and its role in the reproductive behaviour of the cricket *Gryllodes supplicans* (Orthoptera: Gryllidae). *Can. J. Zool.*, 63: 1652 – 1656.
- Sakaluk SK, Schaus JM, Eggert AK, Snedden WA, Brady PL, 2002. Polyandry and fitness of offspring reared under varying nutritional

stress in decorated crickets. *Evolution*, 56: 1999 – 2007.

Sakaluk SK, Smith RL, 1998. Inheritance of male parent investment in an insect. *American Naturalist*, 132: 594 – 601.

Savalli UM, Czesak ME, Fox CW, 2000. Paternal investment in the seed beetle *Callosobruchus maculatus* (Coleoptera: Bruchidae): variation among populations. *Ann. Entomol. Soc. Am.*, 93: 1173 – 1178.

Schaus JM, Sakaluk SK, 2002. Repeatability of sperm number across multiple matings in three cricket species, *Gryllodes sigillatus*, *Gryllus veletis* and *Gryllus texensis* (Orthoptera: Gryllidae). *Can. J. Zool.*, 80: 582 – 585.

Simmons LW, 2001. Sperm Competition and Its Evolutionary Consequences in the Insects. Princeton University Press, Princeton, NJ.

Simmons LW, 2005. The evolution of polyandry: sperm competition, sperm selection and offspring viability. *Annu. Rev. Ecol., Evol. Syst.*, 36: 125 – 146.

Singh SK, Tripathi GM, 2008. Record of sugarcane woolly aphid, *Ceratovacuna lanigera* Zehntner (Homoptera: Aphididae) and its natural enemies in Uttar Pradesh and Uttaranchal. *Resistant Pest Management Newsletter*, 18: 40 – 41.

Slatyer RA, Mautz BS, Backwell PR, Jennions MD, 2012. Estimating genetic benefits of polyandry from experimental studies: a meta-analysis. *Biol. Rev.*, 87(1): 1 – 33.

Souroukis K, Cade WH, 1993. Reproductive competition and selection on male traits at varying sex ratios in the field cricket, *Gryllus pennsylvanicus*. *Behaviour*, 126: 45 – 62.

Srivastava S, Omkar, 2005. Short and long term benefits of promiscuity in a seven-spotted ladybird, *Coccinella septempunctata*. *Int. J. Trop. Insect. Sci.*, 25: 176 – 181.

Torres-Vila LM, Jennions MD, 2005. Male mating history and female fecundity in the Lepidoptera; do male virgins make better partners? *Behav. Ecol. Sociobiol.*, 57: 318 – 326.

Tregenza T, Wedell N, 1998. Benefits of multiple mates in the cricket, *Gryllus bimaculatus*. *Evolution*, 52: 1726 – 1730.

Tregenza T, Wedell N, 2002. Polyandrous females avoid costs of inbreeding. *Nature*, 415: 71 – 73.

Ward PI, Wilson AJ, Reim C, 2008. A cost of cryptic female choice in the yellow dung fly. *Genetica*, 134: 63 – 67.

Wedell N, Ritchie MG, 2004. Male age mating status and nuptial gift quality in a bushcricket. *Anim. Behav.*, 67: 1059 – 1065.

West PM, Packer C, 2002. Sexual selection, temperature, and the lion’s mane. *Science*, 297(5585): 1339 – 1343.

Wilson RS, 2005. Temperature influences the coercive mating and swimming performance of male eastern mosquitofish. *Anim Behav.*, 70(6): 1387 – 1394.

Yasui Y, 1997. A ‘good-sperm’ model can explain the evolution of costly multiple mating by females. *American Naturalist*, 149: 573 – 584.

Yasui Y, 1998. The ‘genetic benefits’ of female multiple mating reconsidered. *Trends Ecol. Evol.*, 13: 246 – 250.

Zeh JA, Zeh DW, 1997a. The evolution of polyandry. I. Intragenomic conflict and genetic incompatibility. *Proc. R. Soc. Lond. B*, 263: 1711 – 1717.

Zeh JA, Zeh DW, 1997b. The evolution of polyandry. II. Post-copulatory defenses against genetic incompatibility. *Proc. R. Soc. Lond. B*, 264: 69 – 75.

# 同时而非先后一雌多雄交配增加不同温度下食蚜瓢虫的适合度

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**摘要:**【目的】尽管一雌多雄在瓢虫科中常见,但各研究中获得的数据不足以解释雌虫多次交配和一雌多雄的一般适应性意义或适合度后果。本研究以温度为胁迫因子,旨在评价一雌多雄的某些益处(如增加的适合度)是否可传递给后代。【方法】本研究检测了黄斑盘瓢虫 *Coelophora saucia* (Mulsant) 3 种交配处理中的适合度:一雌一雄(与同一雄虫交配 5 次,1 次/d),先后一雌多雄(与 5 头不同的雄虫依次交配 5 次,即每天与新的雄虫交配 1 次),以及同时一雌多雄(放进 5 头雄虫,任由雌虫选择雄虫,交配 5 次,1 次/d)。观察了各交配处理不同温度下(25, 27 和 30℃)繁殖力、卵的育性、后代发育和存活。【结果】结果表明,经历一雌多雄然后进行交配选择或竞争的雌性的繁殖能力最强,后代能在更广温度范围内最好地适应发育和存活。但先后一雌多雄交配的雌性与一雌一雄交配的雌性的繁殖能力相似。【结论】结果说明,在无交配选择或雄性竞争的条件下,一雌多雄的益处不明显。这可能是由于在依次射精的雄性间存在精子竞争,或由于雌性的隐性选择。据我们所知,本研究中观察发现的无交配选择时不表现一雌多雄的益处的现象,之前在昆虫中未观察到过。

**关键词:** 瓢虫科; 黄斑盘瓢虫; 一雌多雄; 交配选择; 繁殖能力; 后代适应性

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